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Ornithological surveys in the Cordillera Cocapata, depto. Cochabamba, Bolivia, a transition zone between humid and dry intermontane Andean habitats

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Received 20 April 1998

Recent studies of avian diversity in South America have mainly focused on lowland rainforest and Andean foothills. The analyses by Stotz *et al.* (1996) emphasize the sub-Andean zone as a priority for research and conservation in the light of the habitat changes which are occurring there today. However, this priority does not adequately consider the habitat loss which took place in the past at much higher altitudes. Fjeldså & Kessler (1996) suggest that Andean habitats above 3,500 m have been strongly influenced by man since early post-glacial times, and that less than 5% of the potential humid woodland habitat is left in this altitudinal zone. In general, the timberline is suppressed by at least 500 altitudinal metres, due mainly to the excessive use of fire to maintain open pasture habitats (Kessler 1995). This widespread degradation and lowering of the timberline in the tropical Andes has led to a considerable decline in population size of many bird species restricted to this ecotonal habitat (Kessler & Herzog 1998).

Other areas with a strong and long-lasting human influence are the montane basins (e.g., Cuzco, Cochabamba) and in particular the transition zone from the humid east-Andean slope to the rainshadowed intermontane valleys. In such places, the highest intensity of human use is centered around the most productive zone on the transition from the strongly mist-influenced upper slopes to the often dry lower slopes

and valley bottoms (*cf.* Huston 1994: 559). These transition zones, which have the best-developed soils and most benign climate, have played a special role in the development of past high-Andean cultures and today appear completely devoid of natural vegetation. This habitat conversion took place largely in pre-Colombian times and therefore is often disregarded (Kessler & Driesch 1993, Chepstov-Lusty *et al.* 1998).

It is of particular interest in this respect that the centres of human cultures in the Andes are often immediately adjacent to peak concentrations of species with restricted distributions. Human settlement and the survival of relict avian taxa may depend on similar ecoclimatic factors (Fjeldså & Rahbek 1999). Using long-term series of meteorological satellite images, Fjeldså *et al.* (1998) found these areas to be characterised by low interannual climatic variability caused by orographic moderation of the climate. Such a situation appears to exist in extreme northern Cochabamba and adjacent La Paz, Bolivia, where the Tunari highland, its northern projection Cordillera Cocapata and the outlying Cordillera de Mosetenes provide shelter against the impact of south polar winds which, albeit brief, have a severe ecological impact in the lowlands and along the humid east Andean (yungas) slopes (Fjeldså *et al.* 1998). Such impacts are assumed to have been a principal cause of vegetational changes in tropical South America during the Pleistocene (Servant *et al.* 1993).

As satellite images and topographic maps showed considerable forest tracts adjacent to intensively cultivated land just north of the Tunari/Cocapata highland, we concluded that this area would be worth a closer study, both in terms of possible new avian taxa and from a conservation perspective. No detailed ornithological data existed from this area apart from specimens collected by G. Garlepp, who reached Cocapata in 1892 from the humid subandean zone, and the type specimen of *Ramphomicron microrhynchum bolivianum*, collected in 1980 by C. Cordier (Schuchmann 1984, Paynter 1992). We here present noteworthy results of ornithological studies in April (SKH), May (all four authors) and November (SKH and JAB) 1997 as well as June 1998 (SKH and JAB) in the Cocapata area.

Study area and itinerary

The Tunari highland north of the city of Cochabamba comprises rugged high-Andean grassland (puna) terrain at 4,000–5,000 m and ends in a jagged northward projection, Cordillera Cocapata (4,200 m), which separates wet, uninhabited outer yungas slopes from the intermontane valleys of the Cotacajes drainage. The study area was situated c. 100 km NW of the city of Cochabamba at the end of a dirt road (Fig. 1). Owing to the benign climate of the Cotacajes drainage, all slopes receiving morning sun had been converted to bushy pasture and agricultural fields. However, humid forest remained on west- and south-facing slopes.

The principal study areas were surveyed intensively from dawn until sunset, walking along trails or randomly through the habitats where

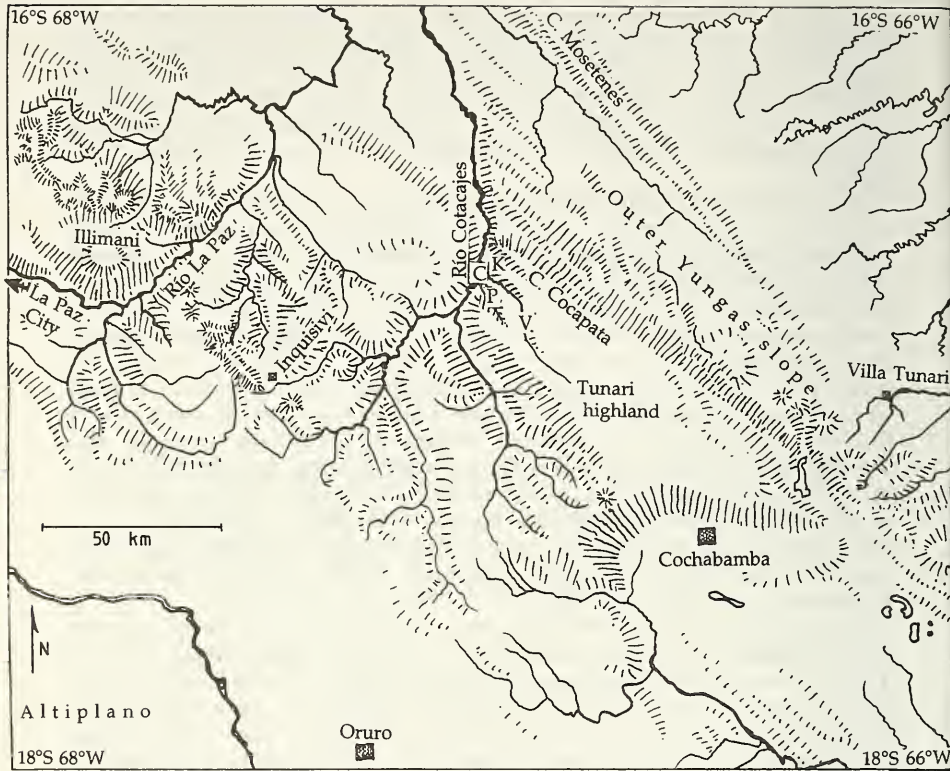


Figure 1. Map of the study area indicating rivers and main topographic features. Locality descriptions are given in the text for C=Cotacajes, P=Pujyani, K=Kori Mayu and V=Casay Vinto.

possible. Most documentation was by tape-recording, but specimens were collected selectively by shooting and low intensity mist-netting. Tape recordings (by SKH) will be deposited at the Cornell Library of Natural Sounds in Ithaca, New York. Specimens are deposited at Colección Boliviana de Fauna in La Paz and the Zoological Museum of Copenhagen.

Survey sites

- (1) *Cotacajes*, depto. Cochabamba, prov. Ayopaya (16°46'S, 66°44'W). A tiny village at the bank of the Río Cotacajes (border to depto. La Paz) at 1,300 m; 26 April, 15–20 May and 12–16 Nov. 1997. The valley bottom was dry upwards from 2 km N Cotacajes with severely degraded dry scrub, whereas our study area at 1,600–2,100 m contained moderately to severely degraded dry forest of 5–8 m height dominated by *Acacia macracantha* and



Figure A. General view of the dry forest zone in the Rio Cotacajes valley from about 2,000 m along the road from Cocapata to Cotacajes, showing the rather open forest structure (visible on the slopes in the background) and the prevalence of columnar cacti (*Cereus huiluncho*) in the foreground.

Prosopis sp. (Fig. A). However, scattered individuals of *Schinopsis brasiliensis*, *Aspidosperma* sp. and *Jacaranda mimosifolia* indicated that the natural vegetation of the area would have consisted of 10–15 m tall semi-deciduous forest. Due to heavy overgrazing by cattle and goats the understory was often rather open and dominated by unpalatable species such as *Croton* sp., *Puya* spp. and various cacti (*Pereskia weberiana*, *Samaipaticereus inquisivensis*, *Cereus huiluncho* and *Opuntia* spp.). Epiphytic plants were rather weakly developed and consisted mainly of atmospheric *Tillandsia* (*T. streptocarpa*, *T. tenuifolia*, *T. bryoides* and others), the climbing ferns *Microgramma vacciniifolia* and *M. squamulosa* as well as scattered orchids and abundant lichens. At its upper limit (>2,000 m) the forest acquired a more mesic character and became more diverse with several leguminaceous species and almost pure patches of an unidentified Myrtaceae. The understory was locally quite dense with weedy composites and Acanthaceae, while the epiphytic plants were represented by green tank bromeliads (mixed with the grey ones mentioned above), ferns, orchids, some Araceae, a few cacti (including the narrowly endemic *Lepismium paranganiense*) and some mosses and hepatics.

- (2) *Pujyani*, depto. Cochabamba, prov. Ayopaya (16°47'S, 66°42'W). 26 April, 6–19 May and 15–17 Nov. 1997, 27–30 June 1998. In the



Figure B. Partial view of the Pujuni study site (foreground) showing the mosaic of mature forest, secondary forest and agricultural areas. In the background, the typical landscape zonation is evident, with a narrow forested belt at about 2,700 to 3,100 m, bordered below by a densely inhabited agricultural zone and above by artificial grasslands resulting from the burning of the *Polylepis* forest belt. Note the few remnant *Polylepis* trees visible on the slopes and near the summit of the mountain and along the ravine at right.

lower part of this study area (2,500–2,700 m) the forest had been converted mainly to corn fields and cattle pastures, but some steep slopes were more or less densely wooded (Fig. B). By interpolating tree height above and below, this zone would naturally have had the maximum canopy height, possibly exceeding 30 m. Due to past clearing, extensive cattle-grazing and many deep landslides, much of the remaining forest at this altitude consisted of secondary *Alnus* forest of up to 12 m height (25 m *Alnus* and Lauraceae trees in a less disturbed patch). The forest's open structure allowed an exuberant development of climbing vines and lianas as well as tall and often spiny shrubs such as *Barnadesia* sp., making the forest nearly impenetrable.

With increasing elevation, forest cover augmented, although there were still large areas of secondary vegetation, particularly at 2,750–2,900 m. The forest types described below were spatially arranged as a mosaic of small (up to several ha) patches interspersed with different types of disturbed vegetation, which ranged from short-grass cattle pastures to weedy fields with *Cleome* sp. and abundant composites to dense thickets of *Barnadesia* spp., *Verbesina* sp., *Piper* spp., *Miconia* spp. and *Chusquea*. Some patches, which had been allowed to regenerate,

sustained secondary forest trees of 5–10 m height, such as melastomes, *Piper* spp. and Myrtaceae. Scattered larger trees remained within these secondary vegetation types.

Above 2,700 m the forest could be classified as humid montane forest up to 27 m tall, dominated by *Weinmannia fagaroides* and *Cedrela odorata*. Palms (*Ceroxylon vogelianum*) were very rare, while *Podocarpus* was completely absent. Humidity increased from lower to higher altitudes, reaching a maximum in the cloud-condensation zone around 3,100 m. This increase was indicated by a parallel increase in abundance of epiphytes (mosses, liverworts, lichens, ferns, orchids, bromeliads, a few Araceae) and terrestrial herbs, especially ferns and tree-ferns. The forest varied with slope inclination and degree of human disturbance. Forest of gentle slopes had in part been logged selectively and was used for grazing cattle, causing the understorey to be generally open, locally only with mosses and some ferns. Some areas were strongly trampled by cattle while other parts, especially ridges, had few signs of recent grazing but may be grazed periodically. Forests on steep slopes were less disturbed but had a lower and naturally broken canopy and dense stands of *Chusquea* bamboo, due to frequent treefalls and shallow landslides.

Above 3,000–3,200 m humidity decreased and human impact increased again, here mainly in the form of fires. This led to the appearance of low (5–10 m) forest with *Clethra* sp., *Clusia* spp., Ericaceae, *Polylepis racemosa* and in even more degraded areas *Monnina* spp. and *Baccharis* spp. On higher mountains the forest continuum extended up to c. 3,500 m, showing a gradual transition to forest dominated by *Polylepis racemosa*.

- (3) *Kori Mayu*, depto. Cochabamba, prov. Ayopaya (16°45'S, 66°41'W). 27 April and 1–2 May 1997. Due to interference from local inhabitants we had to vacate this survey area (camp site at 2,900 m) without detailed study of its avifauna and habitats. The forest appeared to be similar to the Pujyani locality, but probably more humid.
- (4) *Río Cocapata at Casay Vinto*, depto. Cochabamba, prov. Ayopaya (16°52'S, 66°38'W). 3–5 May 1997. Steep (40–70°) west-facing slopes at 3,200–3,500 m above the river contained several patches of *Polylepis racemosa* forest mixed with various shrubs. The trees were covered in epiphytic bromeliads and liverworts (which is unusual for *Polylepis*). Adjacent slopes were covered by tall, apparently rarely burnt *Festuca* grassland, unlike the usual high Andes tussock grassland. Agricultural activities were largely restricted to shallower and especially to sunny north-facing slopes. These slopes and most areas between this locality and the villages of Kori Mayu and Cocapata were covered by a heavily grazed mosaic of cultivated potato and fallow fields, short-grass (mainly above 3,800 m) or tussock grassland and scattered patches of *Puya* bromeliads or degraded scrub. Some observations were also made in the small settlement of Casay Vinto with dense patches of flowering solanaceous bushes near houses.

Species accounts

BROWN TINAMOU *Crypturellus obsoletus*

This species was heard repeatedly in May and November in the Cotacajes dry forest, which is not its usual habitat (cf. Parker *et al.* 1996).

HOOK-BILLED KITE *Chondrohierax uncinatus*

A bird of the rare dark morph was seen several times up to 3,000 m altitude in May and June at Pujyani.

HORNED CURASSOW *Pauxi unicornis*

This rare and vulnerable species (Collar *et al.* 1992) was known by local people, who gave accurate descriptions of casques brought up by hunters from the enormous uninhabited and forested foothill zone NE of Cotacajes towards Cordillera de Mosetenes, which could be a stronghold for the species. Our survey areas, however, did not contain suitable habitat within the species' elevational range.

STRIPE-FACED WOOD-QUAIL *Odontophorus balliviani*

This little-known species was uncommon at Pujyani and also heard during our short visit at Kori Mahu. Small groups were heard (tape-recorded) but seen only briefly when flushed inside the forest or running across the road. One group was singing regularly at dusk in May from a slope with young secondary scrub above our camp at Pujyani, but the species was also heard from inside forest. The loud and bubbly song of the Stripe-faced Wood-Quail is similar to, but notably faster than, that of the Rufous-breasted Wood-Quail *O. speciosus* (vocalizations of both species are presented by Mayer, 1996), which generally occurs at lower altitudes than the former species. Neither in the Cocapata area, nor at any other of our Bolivian study sites, have we found both species at the same altitude. Our only record of *O. speciosus* in the Cocapata area was a pair heard singing in November by SKH in the Cotacajes dry forest from quite far down-slope, probably somewhere between 1,400 and 1,600 m.

MAROON-CHESTED GROUND-DOVE *Claravis mondetoura*

A male of this little known species was flushed by JF on 2 May 1997 at Kori Mayu. Bamboo, with which this species seems frequently to be associated (Hilty & Brown 1986, Fjeldså & Krabbe 1990, but see Herzog *et al.* 1997), was flowering locally in the whole area.

LARGE-TAILED DOVE *Leptotila megalura*

This was the only species of the genus *Leptotila* we recorded in the Cocapata area, where it was common at Cotacajes and uncommon at Pujyani. Surprisingly, we did not find the White-tipped Dove *L. verreauxi* in the Cotacajes dry forest. *L. verreauxi* is usually a common inhabitant of Andean dry forest throughout Bolivia and often sympatric with *L. megalura*, e.g., both in the La Paz valley further north and in parts of the dry valles region of the southern Bolivian Andes (Herzog

et al. 1997, SKH and MK unpubl. data). In contrast to this sympatry, JF found a clear habitat separation between the two species in southern depto. Chuquisaca (see Fjeldså & Mayer 1996), with *megalura* occupying islands of evergreen or semi-evergreen forests and *verreauxi* the more widespread deciduous forest. Apparently, the distribution and ecological differentiation of these two closely related species do not follow a simple, easily predictable pattern but vary regionally.

GREEN-CHEEKED PARAKEET *Pyrrhura molinae*

All individuals observed (and collected) belonged to the nominate subspecies. Thus, the distinctive and recently described *P. m. flavoptera* (Maijer et al. 1998) is probably restricted to the upper parts of the Cotacajes drainage and the adjacent La Paz valley. Since there appear to be no ecological or geographical barriers separating the two forms in the Cotacajes drainage (*P. m. flavoptera* has been found 30 km to the SW in the same valley system in similar habitat by N. Krabbe (Borgtoft et al. 1999)), the factors determining the distribution and differentiation of the two subspecies remain unknown.

RUFIOUS NIGHTJAR *Caprimulgus rufus*

One individual was heard singing by SKH after dusk on 12 November 1997 at 2,050 m in the Cotacajes dry forest, which represents the second observation from depto. Cochabamba as well as a new altitudinal record for the species (see also altitudinal records below). The first record for depto. Cochabamba was obtained by SKH on 22 September 1997 below Cerro Leñe in the northeastern corner of Parque Nacional Carrasco (17°23'S, 64°24'W), where a single bird was tape-recorded inside primary, unbroken, humid lower foothill forest at 500 m. Humid foothill forest is quite an unusual habitat for this species which, in Bolivia, generally inhabits drier and more open forest and woodland habitats in the chaco, cerrado and valles regions (Armonía 1995, Parker et al. 1996).

BLUE-CAPPED PUFFLEG *Eriocnemis glaucopoides*

This generally rare and local species was fairly common in May both at the Río Cocapata and Pujyani and was collected at both sites. However, it was not observed during the shorter November visit. These are the northernmost records for the species, and the record at 3,400 m at the Río Cocapata also represents an upward altitudinal range extension by 500 m (cf. Fjeldså & Krabbe 1990, Parker et al. 1996). S. Maijer (pers. comm.) had previously found the species as far north as Cerro Chojna Khota (16°52'S, 67°13'W) near Inquisivi, prov. Inquisivi, depto. La Paz, where he observed two males in a humid forest clearing at 2,900 m on 8 December 1993. This represents the first observation of Blue-capped Puffleg in depto. La Paz (cf. Remsen & Traylor 1989, Armonía 1995).

PURPLE-BACKED THORNBILL *Ramphomicron microrhynchum*

Several birds displaying female plumage characteristics were seen in low shrubbery (mainly *Cleome* sp.) by JF at Kori Mayu and Pujyani,

but never well enough to determine the subspecific affinity. Cocapata is the type locality for *R. m. bolivianum* (Schuchmann 1984) and the only known locality of this subspecies.

SCALED METALTAIL *Metallura aeneocauda*

A single individual seen on 4 May 1997 by JF at the Río Cocapata fills in a distributional gap between the nominate subspecies of the Peruvian yungas and La Paz, Bolivia, and the isolated subspecies *malagae* from Incachaca to Siberia, depto. Cochabamba. The subspecific affinity could not be determined in the field.

HOODED MOUNTAIN-TOUCAN *Andigena cucullata*

This near-threatened species (Collar *et al.* 1992) was surprisingly common in the Pujyani humid montane forest with at least ten individuals in the main survey area of about 2 km².

STRONG-BILLED WOODCREEPER *Xiphocolaptes promeropirhynchus*

Common at Pujyani, one or two individuals were also observed in May around 2,050 m in the Cotacajes dry forest, where this species is apparently sympatric with the Great Rufous Woodcreeper *X. major*. The song of probably the latter species was heard once in May by SKH from the lower half of the Cotacajes study site. In November the Great Rufous Woodcreeper was occasionally heard singing at Cotacajes and once seen by JAB at 2,050 m. However, *X. promeropirhynchus* was not observed in the dry forest in November.

SOOTY-FRONTED SPINETAIL *Synallaxis frontalis*

In September 1995 an undescribed subspecies of *S. frontalis* (to be described separately) was found by SKH and MK in the upper Cotacajes drainage near Inqusivi (16°54'S, 67°09'W). Similar individuals were also found (collected and tape-recorded) in the Cotacajes dry forest. Here, around an altitude of 2,000 m, *S. frontalis* was syntopic with *S. azarae* (*superciliosa*), with *frontalis* occupying the drier forest below and *azarae* the more mesic forest above 2,000 m and the two differed vocally.

The primary vocalization (song) of both species is a nasal, two-noted "ka-kweek", in which the second note is slightly higher-pitched and longer in duration than the first note. A frequency analysis, however, showed that the song of *frontalis* was higher in pitch than that of *azarae* (frequency range of "typical" songs 4.3–6.0 kHz *vs.* 3.5–5.2 kHz, respectively, an easily audible difference) and that both notes of the song of *frontalis* had a very similar or identical amplitude (volume), whereas in *azarae* the first note always had a significantly lower amplitude than the second note. Additionally, each species had its "own" vocalizations that were not heard from their congener. *S. azarae* uttered series of scratchy, somewhat rubbery and nasal "prrrt" notes occasionally interspersed with a fast, nasal "kweek-kweek" or "kweek-kweek-kweek". These vocalizations were also heard at Pujyani where *S. frontalis* did not occur. *S. frontalis* gave series of nasal and somewhat soft "tweet" calls with some variation in tone and pitch.

BOLIVIAN SPINETAIL *Cranioleuca henricae*

Observed at 1,800–2,050 m in the Cotacajes dry forest in May (in mixed feeding flocks) and November (when also collected and tape-recorded; territorial pairs and an apparently single bird joining a mixed flock moving through its territory). This represents the first record of this recently described species (Majer & Fjeldså 1997) for depto. Cochabamba as well as the lowest altitudinal record.

LIGHT-CROWNED SPINETAIL *Cranioleuca albiceps*

Both the white-crowned northern subspecies (*C. a. albiceps*) and the buff-crowned southern subspecies (*C. a. discolor*) were found and collected in the Pujyani survey area. Intermediate individuals were also collected. These subspecies have previously been thought to be separated by the La Paz/Cotacajes drainage system (Fjeldså & Krabbe 1990), but our findings suggest an introgression of *albiceps* into extreme northern Cochabamba. Vocally, both subspecies appeared to be similar.

SHORT-TAILED ANTHRUSH *Chamaeza campanisona*

Several singing individuals were observed (tape-recorded) in November around 2,050 m in the most humid part of the Cotacajes dry forest, which is presumably not its usual or preferred habitat (*cf.* Ridgely & Tudor 1994, Parker *et al.* 1996). Here the species appeared to favour forest with dense understorey and patches of dense scrub. At Pujyani this species occurred to at least 2,800 m (see altitudinal records below) and was sympatric with the Barred Anthrush *C. mollissima*.

SCALED ANTPITTA *Grallaria guatimalensis*

This species was observed only in November in dry and humid forest up to 2,800 m (where replaced by Undulated Antpitta *G. squamigera*). The intensive survey effort in May and repeated observations of the other *Grallaria* species during this time indicate that the species may have been absent or at least rare in May, suggesting local migration.

SUIRIRI FLYCATCHER *Suiriri suiriri*

One or two were tape-recorded on 17 May 1997 in the Cotacajes dry forest, but the species was not encountered in November, suggesting that the birds observed in May represented austral migrants. As the birds were heard only, the subspecific affinity could not be determined. The Suiriri Flycatcher has also been found even further north in the Andes at Cerro Asunta Pata (15°03'S, 68°28'W) in depto. La Paz by SKH, where two birds were tape-recorded (but not seen) on 22 June 1997 at 1,350 m in evergreen forest. This probably represents the first record of this species for depto. La Paz (*cf.* Remsen & Traylor 1989, Armonia 1995, Chesser 1997) and the northernmost observation for the Andes. These individuals are also believed to represent austral migrants.

HIGHLAND ELAENIA *Elaenia obscura*

This species was observed only in November in the dry forest, where it was common at 2,000–2,100 m. Its apparent absence in May suggests

local movements. Despite the presence of suitable habitat, especially in the lower part of the Pujyani study site, located well within the species' altitudinal distribution, it was not encountered here.

Cnemotriccus sp.

An apparently undescribed species, closest to the Fuscous Flycatcher *Cnemotriccus fuscatus*, was found to be uncommon in the dry forest at 1,650–2,050 m. Three specimens were collected. This form had previously been collected in depto. La Paz in 1938 by the Olalla family (see Fjeldså & Krabbe 1989, where these specimens were erroneously referred to *C. fuscatus bimaculatus*) and in 1993 (S. Cardiff and J. V. Remsen, in litt). The taxon will be described and named elsewhere.

RUFOUS-BELLIED BUSH-TYRANT *Myiotheretes fisorufus*

This near-threatened species (Collar *et al.* 1992) was surprisingly common in the Pujyani humid montane forest with up to ten individuals along a 2 km stretch of road.

WHITE-TAILED SHRIKE-TYRANT *Agriornis andicola*

An individual seen on 3 May 1997 by SKH and MK represents the first observation of this threatened species (Collar *et al.* 1992) for depto. Cochabamba (*cf.* Remsen & Traylor 1989, Armonía 1995). It was perched openly on a *Puya* inflorescence on a slope with a large *Puya* population along the road between Casay Vinto and Cocapata at about 3,500 m.

BLUISH FLOWERPIERCER *Diglossa caerulescens*

Several sightings of this species in the Pujyani humid montane forest in May 1997 by SKH and JF represent the first observations of this species in depto. Cochabamba (*cf.* Remsen & Traylor 1989, Armonía 1995).

Diglossa sp.

An apparently all black flowerpiercer, which almost certainly represents an undescribed taxon, was seen several times in the Pujyani humid montane forest between 2,700 and 3,100 m in May 1997 by all four authors. Size and shape suggested that it may be related to the Moustached Flowerpiercer *D. mystacalis* which, albeit being common in comparable habitat further north and south, has not been recorded in the study area. Birds were always in pairs in mixed foraging flocks in the upper canopy. No specimen has yet been collected.

THICK-BILLED SISKIN *Carduelis crassirostris*

A single juvenile was seen by SKH and JAB on 30 June 1998 at 2,600 m in secondary humid scrub in the Pujyani survey area. The bird was apparently moving uphill but paused for about one minute, perching openly 5 m up on top of the vegetation and giving a few single-note calls. This uncommon and local species inhabits *Polylepis* woodlands and arid montane scrub at altitudes above 3,000 m (Ridgely & Tudor 1989, Fjeldså & Krabbe 1990, Parker *et al.* 1996). The bird

was probably performing short-term altitudinal migration in response to a southern storm front with heavy rainfall and snowfall above 4,000 m (see O'Neill & Parker 1978), which had occurred from 23–26 June 1998 in the Cochabamba area.

OLIVACEOUS SISKIN *Carduelis olivacea*

This species was found only in November both in humid and dry forest. In the dry forest a group of three and a single female were seen perched in the canopy, whereas at Pujyani several flocks of up to 20 birds were observed moving through the upper level of semi-open and moderately degraded forest. The Hooded Siskin *C. magellanica*, of which *C. olivacea* may only be a subspecies (see Ridgely & Tudor 1989), was common in the Casay Vinto area and not found at Pujyani, suggesting that the two taxa are separated altitudinally in the Cocapata area.

Discussion

We recorded 229 bird species in the Cocapata area, 86 of which were observed in the Cotacajes dry forest, 138 at Pujyani, 59 at Kori Mayu and 58 in the Casay Vinto area. Ten species (*Buteo magnirostris*, *Columbina picui*, *Claravis mondetoura*, *Uropsalis* cf. *segmentata*, *Colibri serrirostris*, *Patagona gigas*, *Coeligena torquata*, *Sappho sparganura*, *Catamenia inornata* and *Thraupis sayaca*) were present at Kori Mayu but not found at Pujyani, resulting in a total of 148 species for the humid montane forest zone in the Cocapata area. A complete species list including relative abundances and evidence is presented in Borgtoft *et al.* (1999).

Many species reached exceptionally high altitudes in the Cocapata area with the majority of them recorded at Pujyani, and a complete list of these species is presented below. The highest observed altitude is given in parentheses behind each species' name, followed by the previously known upper altitudinal limit. Unless indicated otherwise, previously known altitudinal limits are based on Ridgely & Tudor (1989), Fjelds  & Krabbe (1990), Ridgely & Tudor (1994), Armon a (1995) and Parker *et al.* (1996): *Chondrohierax uncinatus* (3,000/2,800 m, however, in Colombia rarely to 3,100 m, Fjelds  & Krabbe 1990), *Micrastur ruficollis* (2,800/2,600 m), *Geotrygon frenata* (3,200/3,000 m, but recorded up to 3,350 m in PN Carrasco, SKH and MK, unpubl. data), *Brotogeris chiriri* (1,850/1,200 m, but in the dry valleys of the Bolivian Andes reaching at least 2,350 m, see Herzog *et al.* 1997, SKH and MK, unpubl. data), *Caprimulgus rufus* (2,050/1,700 m), *Eriocnemis glaucopoides* (3,400/2,900 m), *Aulacorhynchus coeruleicinctus* (2,900/2,700 m), *Xiphocolaptes major* (2,050/1,800 m), *Chamaeza campanisona* (2,800/2,350 m, Fjelds  & Mayer 1996), *Scytalopus bolivianus* (2,500/2,300 m), *Mecocerculus hellmayri* (3,050/2,600 m), *Contopus fumigatus* (3,000/2,600 m), *Contopus cinereus* (2,850/2,200 m), *Myiodynastes chrysocephalus* (2,750/2,500 m), *Chiroxiphia boliviana* (2,600/2,500 m), *Sporophila caerulescens* (2,800/2,500 m), *Chlorospingus ophthalmicus* (3,050/2,600 m), *Hemispingus melanotis* (2,850/2,700 m),

Anisognathus flavinucha (2,950/2,500 m), *Pipraeidea melanonota* (2,850/2,500 m), *Tangara xanthocephala* (2,700/2,400 m), *Tangara ruficervix* (2,850/2,400 m), *Tangara cyanotis* (2,800/2,200 m), *Basileuterus signatus* (3,050/2,800 m), *Psarocolius atrovirens* (3,000/2,800 m) and *Psarocolius angustifrons* (2,800/2,400 m).

We believe that our record of the resident avifauna is almost complete, at least for the main ecological zones of our study. The following species of humid yungas forest appear to be genuinely absent from our study area: *Oroaetus isidori*, *Adelomyia melanogenys*, *Heliangelus amethysticollis*, *Pharomachrus* spp., *Grallaria albigula* and *erythrotis*, *Thripadectes scrutator*, *Knipolegus signatus*, *Pachyramphus versicolor*, *Pseudotriccus ruficeps*, *Cinnycerthia fulva* and *Cacicus holosericeus*. It is more remarkable, however, how many humid-slope species were present, some of them even in the Cotacajes dry forest (mainly in humid ravines; *Crypturellus obsoletus*, *Penelope montagnii*, *Odontophorus speciosus*, *Columba fasciata*, *Hapalopsittaca melanotis*, *Amazona mercenaria*, *Chamaeza campanisona*, *Grallaria squamigera*, *Phyllomyias sclateri*, *Elaenia obscura*, *Mecocerculus leucophrys*, *Contopus fumigatus*, *Myiarchus cephalotes*, *Chlorospingus ophthalmicus*, *Chlorophonia cyanea* and *Carduelis olivacea*).

The following intermontane basin endemics were not found in the Cocapata area but, although not necessarily restricted to higher elevations, have isolated populations at the upper reaches of the Cotacajes/La Paz drainages: *Pyrrhura molinae flavoptera*, *Lesbia nuna*, *Asthenes heterura*, *Mimus dorsalis*, *Saltator rufiventris*, *Atlappetes fulviceps*, *Poospiza boliviana* and *P. whittii*.

The favourable ecoclimatic conditions north of the Tunari highland (maybe reaching up to northern La Paz) could explain the occurrence of an isolated population of *Ramphomicron microrhynchum bolivianum*, an endemic subspecies of *Synallaxis frontalis* as well as endemic species (*Craniroleuca henricae*, *Cnemotriccus* unnamed sp., *Diglossa* unnamed sp.) in our survey area.

In the Pujyani and Kori Mayu humid forest we recorded 148 species between 2,500–3,200 m with a survey effort of 41 observer days. In comparison, only 111 species were found within the same altitudinal range on the outer yungas slope above Villa Tunari 90–120 km to the SE. This latter figure is comprised of the combined number of species at two localities, namely western Parque Nacional Carrasco (17°11'–13'S, 65°40'–41'W, 2,500–3,200 m, two visits by SKH and MK, 16 observer days) and Tablas Montes (17°15'S, 65°10'W, 2,600–3,000 m, three visits by JF, 14 observer days, one visit by B. Hennessy (in litt.), 2 observer days). Our study area in the Cordillera Cocapata was 5–10 km away from the nearest wet outer yungas slope with ecoclimatic conditions similar to those above Villa Tunari.

The striking difference in species richness between the two areas is probably caused mainly by two factors. Firstly, the evergreen forest zone of Pujyani certainly receives much less precipitation than the extremely wet Villa Tunari area (present authors). Excessive moisture as observed in the Villa Tunari area is considered to have a negative

impact on vegetation development (Ellenberg 1975). Moreover, less precipitation and hence less cloud cover at Pujyani cause higher temperatures, higher solar insolation and, provided the minimum amount of moisture necessary to maintain evergreen forest is present, higher productivity of the vegetation at the same altitude. This in turn allows the development of taller, structurally more complex forest which may allow many submontane bird species, whose elevational distribution may be determined by habitat structure rather than elevation *per se*, to reach exceptionally high altitudes at Pujyani (see above). Of course, a further reduction in precipitation would result in lower, more deciduous forest with a significantly lower bird diversity. Secondly, the proximity of other habitats (dry forest, barren intermontane and agricultural habitats), which are absent from the outer yungas slope, also contribute to the avian species richness in the humid forest. Species such as *Columbina picui*, *Sappho sparganura*, *Knipolegus aterrimus*, *Turdus chiguanco*, *Saltator aurantirostris* and *Myioborus brunniceps* were not recorded in our survey areas above Villa Tunari but occurred at Pujyani and/or Kori Mayu.

The outer yungas slope to the NE of the Tunari highland, especially at the northern end of the Cordillera Cocapata, still supports a continuous altitudinal gradient from humid montane forest to high-altitude scrub and grassland and hence would be a highly interesting study area, even though access would be very difficult.

Acknowledgements

For good companionship in the field we would like to thank A. Acebey, K. Bach, J. Bolding, M. del Carmen Ramirez, D. Goffard, J. Gonzales and M. Olivera. A. J. Bolding prepared the majority of the specimens and significantly contributed to the well-being of everybody at Schwudelbau Camp during the main survey work in May 1997. The usual thanks go to the staff of the Colección Boliviana de Fauna, especially C. Quiroga O., in La Paz for work permits and logistical support. For logistical help in Cochabamba we are especially grateful to S. Arazola. Financial support for the field work was provided by the DIVA project under the Danish Environmental Programme (SKH, JF and JAB), the Deutscher Akademischer Austauschdienst (German Academic Exchange Service, to SKH in 1998), Fauna & Flora International (to SKH and JAB in 1998) and the Deutsche Forschungsgemeinschaft (German Research Association, to MK).

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Subspeciation in the Australian-endemic Great Bowerbird *Chlamydera nuchalis* (Ptilonorhynchidae): a review and revision

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Received 1 July 1998

The Great Bowerbird *Chlamydera nuchalis* is an endemic Australian polygynous species. It occurs across tropical northern and north-eastern Australia, from the western Kimberley of Western Australia eastward to the Queensland coast, and thence northward to Cape York on northern-most Cape York Peninsula, and southward in eastern Queensland to areas of the upper Burdekin River/Mackay (Fig. 1). It belongs to the only bowerbird genus adapted to relatively dry, sparsely-vegetated habitats, where it frequents riverine woodlands and vine thickets, eucalypt and melaleuca woodlands, open savannah woodlands and planted suburban areas.

Adult males and females have almost identical plumage, in variable warm greys to brown-greys throughout head, neck and underparts, with upperparts pale (in west and north) to dark (in east) blackish-brown, with extensive broad whitish tipping and edging to all feathers below the nape. Subadult to adult males and a few (? older) females have the upper nape supporting a nuchal crest of erectile silky pink feathers. Immatures and females of some populations show conspicuous ventral barring, particularly on the flanks, which is only faintly discernible on older birds and is absent on adult males. Plumages remain inadequately understood owing to insufficient numbers of specimens from several localities for each named subspecies, sex, age class, month, and because of complicating variation in plumage wear (Mayr & Jennings 1952). For detailed plumage descriptions, and/or illustrations of them, see Mayr & Jennings (1952), Marshall (1954), Gilliard (1969), Cooper & Forshaw (1977) and Donaghey (1996).

To facilitate easier comprehension of subsequent text a summary of more significant Great Bowerbird subspecies descriptions, and brief plumage diagnosis of them (after Gilliard 1969), follows. The